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# Patterns of temperature induced developmental plasticity in anuran larvae

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ABSTRACT

Anurans exhibit plasticity in the timing of metamorphosis and tadpoles show phenotypic plasticity in age and size at metamorphosis as a response to temperature variation. This developmental plasticity to changing thermal conditions is expected to be a primary factor that dictates the vulnerability of amphibians to increasing ambient temperatures such as are predicted in climate change scenarios. We analyzed the patterns of thermal effects on size and age at metamorphosis to investigate whether the intraspecific "temperature-size rule" is applicable over a broad range of anuran species by carrying out a combined analysis based on the data from 25 studies performed on 18 anuran species. Furthermore, we tested whether the thermal background of respective populations impacts the capacity for a plastic response in metamorphic traits. We could confirm this pattern for across-population comparisons. All included populations developed faster and 75% were smaller at the onset of metamorphosis when developmental temperatures were warmer, but the sensitivity of growth and developmental rate to a given temperature change was different. We found that the thermal background of a population influences the sensitivity of metamorphic traits and thus, the capacity for a plastic response in growth and developmental rate. Warm adapted populations were less sensitive to temperature variation indicating a reduced capacity for developmental plasticity and therefore, those species may be more vulnerable to the impacts of climate change. Future studies should include a broader range of rearing temperatures and temperature fluctuations to determine full knowledge of the capacity for developmental plasticity within a species-specific thermal window.

## 1. Introduction

Species are declining worldwide due to habitat loss, disease, and environmental variation as caused by both natural and anthropogenic global environmental change (Stuart et al., 2004; Strong et al., 2017). In organisms with complex life cycles such as holometabolous insects, marine invertebrates, parasites, most teleost fish, and amphibians changing environmental conditions lead to a plastic response in their timing of metamorphosis (i.e. plastic growth and developmental rate) (Wilbur, 1980; Pechenik et al., 1998; Rudolf and Rödel, 2007; Laudet, 2011). Depending on the taxa, metamorphosis can cause a life-history transition that involves radical changes in habitat, morphology, and physiology. Thus, the timing of metamorphosis is of key importance for the entire life history and population dynamics (Walters and Hassall, 2006; Rudolf and Rödel, 2007). For organisms that live in temporally and spatially heterogeneous environments, phenotypic plasticity in age and size at metamorphosis may provide a means for increasing fitness in later life stages (Schlichting and Pigliucci, 1998; Boorse and Denver, 2004). For example, in amphibians, traits such as short larval period and large size at metamorphosis are assumed to confer greater fitness (Wilbur and Collins, 1973; Beck and Congdon, 2000).

Larval amphibians are especially sensitive to environmental variation due to their life history (Searcy et al., 2015), their highly permeable skin (Yu et al., 2015; Strong et al., 2017), and their limited capacity for habitat selection (Sanzo and Hecnar, 2006; Yu et al., 2015). Amphibians exhibit plasticity in the timing of metamorphosis and tadpoles show phenotypic plasticity in the larval stage in general, but especially in age and size at metamorphosis (Wilbur and Collins, 1973; Newman, 1992; Denver et al., 1998; Boorse and Denver, 2004). Different studies demonstrated a plastic response of metamorphic traits in anuran larvae to changes in environmental conditions such as crowding (Ding et al., 2015), presence of predators (Relyea and Hoverman, 2003; Relyea, 2003), food quality and quantity (Courtney Jones et al., 2015), photoperiod (Laurila et al., 2001), desiccation (Gervasi and Foufopoulos, 2008), water quality (Calich and Wassersug, 2012), and temperature (Vences et al., 2002).

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As amphibians are ectotherms, temperature is one of the major abiotic factors influencing metamorphosis. This can be directly related to the thermal sensitivities of the rate of biochemical and physiological processes that underlie morphogenesis (Smith-Gill and Berven, 1979; Hayes et al., 1993; Denver et al., 1998; Little and Seebacher, 2016). Plasticity in age and size at the onset metamorphosis results from plastic responses of somatic growth of existing tissues and of the developmental rate of new tissues (Newman, 1992; Chambers and Leggett, 1992). These two processes can, to some extent, be decoupled by environmental factors (Zuo et al., 2012; Walters and Hassall, 2006; Gomez-Mestre et al., 2010).

The plasticity in growth and development can be explained by the intraspecific "temperature-size rule" (TSR), which predicts that ectothermic species, including amphibians, reared at relatively lower temperatures display slower growth rates but a prolonged larval period and thus, typically mature later at larger sizes when compared with conspecifics reared at higher temperatures (Atkinson, 1994; Angilletta et al., 2004; Courtney Jones et al., 2015). Walters and Hassall (2006) emphasized that developmental rate is more sensitive to increasing temperatures than growth rate due to differential effects on anabolism and catabolism (von Bertalanffy, 1960; Angilletta and Dunham, 2003). Therefore, a higher temperature affects the development stronger than the growth rate (Gomez-Mestre et al., 2010).

For the TSR an optimal thermal range exists and this is bordered by a suboptimal range in which age and size plasticity does not occur (i.e. extreme conditions at which size decreases significantly) (Walczyńska et al., 2016) and thermal limits, which are usually defined by the critical thermal minimum ($CT_{min}$) and maximum ($CT_{max}$) in amphibians (Cowles and Bogert, 1944; Lutterschmidt and Hutchison, 1997; Turriago et al., 2015). The magnitude and direction of the response to temperature is species- and population-specific and depends on the range in thermal tolerance (Freitas et al., 2010). Adaptive shifts in the thermal range of tolerance (i.e. thermal adaptation) can result from biological processes that occur over longer time scales (Angilletta et al., 2002). Pörtner et al. (2006) uses "thermal windows" as an alternative term for the range of thermal tolerance of growth and development for all aquatic taxa but not for anurans which usually have a semiaquatic life-history. However, in most cases a tadpole's mode of life is entirely aquatic. Therefore, we suggest equally using the term "thermal windows" to describe the range of temperatures suitable for the development of anuran larvae. The thermal window in amphibians is generally related to the geographic and altitudinal distribution of the species (Turriago et al., 2015). In ectotherms, it is relatively broad in temperate species, narrower in tropical species and most narrow in species found only in polar areas (Huey and Kingsolver, 1993; Angilletta et al., 2002; Pörtner and Peck, 2010; Berg et al. 2017). In tadpoles, the width of thermal windows increases from tropical to temperate latitudes due to an increasing cold tolerance (Gutiérrez-Pesquera et al., 2016).

Temperatures beyond this species- or population-specific thermal window proximately cause stress which alters tadpoles' hormonal balance by activating the neuroendocrine stress axis (Wilbur and Collins, 1973; Berven and Chadra, 1988; Laudet, 2011; Navas et al., 2016). As metamorphosis is a process driven by thyroid hormones (TH), stress hormones may interact with TH resulting in increased TH production (Laudet, 2011; Glennemeier and Denver, 2002) and thus, lead to an increased developmental rate. Consequently, the rate of metamorphosis is in two respects influenced by the ambient temperature: through physiological and endocrine mechanisms which result in plastic responses of growth and developmental rate (Smith-Gill and Berven, 1979; Denver et al., 1998; Courtney Jones et al., 2015).

This considerable impact of temperature on growth and development during the larval stage and therefore, on fitness in later life stages, takes on greater significance in terms of the ongoing global climate change: The frequency of extreme thermal events (temperature peaks beyond $CT_{max}$ of many species, increased desiccation risk, and increased mean annual temperatures) will increase in the future in all climate zones (Pachauri et al., 2014; Gutiérrez-Pesquera et al., 2016). Rijnsdorp et al. (2009) and Mehner et al. (2011) emphasize that knowledge on the thermal window of organisms is fundamental to understand the response of populations to global warming. Numerous studies on anuran larvae investigated the effect of temperature on growth and developmental rate and thus, on age and size at the onset of metamorphosis. However, these studies refer to the species-specific effect of temperature during the larval period (Smith-Gill and Berven, 1979; Àlvarez and Nicieza, 2002; Walsh et al., 2008; Dittrich et al., 2016; Courtney Jones et al., 2015; Gutiérrez-Pesquera et al., 2016). Even if amphibian larvae are generally known to develop at different rates and metamorphose at different sizes within their thermal windows, across-species comparisons, which allow for projections on the impact of climate change, are rare.

In this paper, we examine whether there is a general pattern of thermal effects on age and body size at the onset of metamorphosis in anuran larvae. We perform a combined analysis based on a total of 25 studies from 18 articles published between 1988 and 2016. This analysis aims to examine whether the "temperature-size rule" is not only applicable to intraspecific but also to interspecific comparisons of different anuran species. We specifically investigated (1) the effect of rearing temperature on metamorphic traits within and across all included populations, and (2) how the thermal background of the respective populations impacts the sensitivity of growth and developmental rates to different rearing temperatures. Furthermore, we review the potential consequences of temperature-driven plastic responses in rates of growth and development of pre- and pro-metamorphic larvae to post-metamorphic and adult life stages. This synthesis reveals whether common patterns exist among species-specific thermal effects on metamorphic traits which would allow more robust projections on the impacts of climate change at individual and population level.

## 2. Material & methods

### 2.1. Systematic literature review

We did a systematic literature review using ISI Web of Science (ISI WOS, 2017) in January 2017 (searched for: "**TOPIC**"; search term: (("amphibian larvae" OR "anuran larvae" OR "tadpoles") AND ("thermal" OR "temperature" OR "environment*" OR "abiotic" OR "biotic" OR "climat* change" OR "climat* shift" OR "acidification" OR "pH" OR "predator" OR "density" OR "desiccation") AND ("effect*" OR "impact*" OR "cause") AND ("growth" OR "development*") AND (rate OR time) AND ("larval time" OR "larval duration" OR "larval period") AND (development* window OR "thermal window") AND ("development* plasticity" OR "growth plasticity" OR "plasticity metamorphosis") AND ("size" OR "time" OR "age") AND ("metamorphosis")); Timespan**:** All years.) (Pullin and Stewart, 2006). The systematic literature review returned 1236 articles into an unfiltered reference library. After examining titles and abstracts, 523 articles were left as possibly relevant in the filtered reference library. Examining the full text of the filtered reference library led to 18 articles accepted in the reference library. The following selection criteria had to be fulfilled by the experimental design of the included studies: (1) experiments were conducted in the laboratory (no field studies), and (2) at least at two different rearing temperatures for the tadpoles. These articles were published between 1988 and 2016 (with 55% of the studies published during the past 10 years) and comprised 25 individual studies representing 25 amphibian populations, which were included as replicated in the analysis. These 25 populations were from 18 species, 12 genera and 7 families according to the Linnean classification.

### 2.2. Data collection

For each population we extracted results for age (days after hatching to onset of metamorphosis), and size at onset of

metamorphosis and $T_{rear}$ as rearing temperature (i.e. tested temperature points) used in the respective studies. Size was measured by mass (mg), and snout-vent length (SVL; mm). Rearing temperatures reached from 10 to 33 °C (Appendix Table A.1). The onset of metamorphosis was defined as the emerging of at least one forelimb according to Gosner developmental stage 42 (Gosner, 1960). For studies which use figures instead of tabularization of their results we used Engauge Digitizer 9.7 to extract data from the graphs. Different sample sizes for independent variables mass, SVL, and age at metamorphosis result from studies which include not all of the three variables.

### 2.3. Thermal background

From each study we extracted information on the respective spawn collection site as detailed as possible. To investigate the thermal adaption of the population to the climate of spawn collection site we listed average annual temperature ($T_{average}$), temperature of the coldest ($T_{CM}$) and hottest ($T_{HM}$) month of the respective spawn collection site using the database of Climate-Data.org (Climate data, 2017). We used macroclimate data (i.e. non-buffered air temperature) as a proxy to estimate the thermal adaptation for the respective populations due to the lack of the microclimate data (e.g., actual water temperatures in the breeding pond) in original articles. We are aware of the restriction when predicting the impacts of climatic change using macroclimate data, because understanding the way that microenvironments filter environmental fluctuations is crucial for amphibian larvae inhabiting fluctuating microhabitats (Woods et al., 2015; Oyamaguchi et al., 2017). Temperatures at spawn collection sites reached from 0.5 to 26.5°C for the average annual temperature, from 13 to 31°C for the hottest month, and -13–25 °C for the coldest month (Appendix Table A.1).

### 2.4. Statistical analysis

All statistical tests were carried out in the R environment (R 3.4.1; R Development Core Team, 2007) for Windows and plots were constructed using ggplot2 (Wickham, 2009) and Adobe Illustrator CS6.

#### 2.4.1. Effect of temperature on metamorphic traits

We used a plasticity index (PIX) that describes the change in in metamorphic traits with a given change in rearing temperature (Appendix Table A.1). This PIX was determined by performing linear regressions of rearing temperature (independent variable) and metamorphic traits (dependent variables) for individual populations (Fig. 1) and using the slope to determine the effect of rearing temperature on metamorphic traits (as measured by SVL, mass, and age). PIX values indicate the sensitivity of growth and developmental rate to different rearing temperatures, and thus, the ability for a plastic response in metamorphic traits. Values for SVL, mass, and age were log-transformed to account for high levels of regression residuals.

#### 2.4.2. Effect of thermal adaptation on

To examine the effect of the thermal background on metamorphic traits (i.e. the plasticity index of SVL, mass, and age at the onset of metamorphosis) data were analyzed using linear mixed-effect models [lme, Type III model, covariance type: variance components, REML (restricted maximum likelihood) method for parameter estimation, 100 iterations (Bates and Sarkar, 2007)], using the covariates '$T_{CM}$' and '$T_{HM}$' as fixed factor. The plasticity indices for log-transformed SVL, mass, and age at the onset of metamorphosis were used as dependent variables in three separate models (Table 1). P-Values were obtained from likelihood-ratio tests, which compared the models with the respective null-model (Crawley, 2007). To avoid pseudoreplication and to correct for phylogenetic differences, the variables 'population', 'species', 'genus', and 'family' were included as a nested random factor. Although the number of species is moderate (N = 18) this is close to the

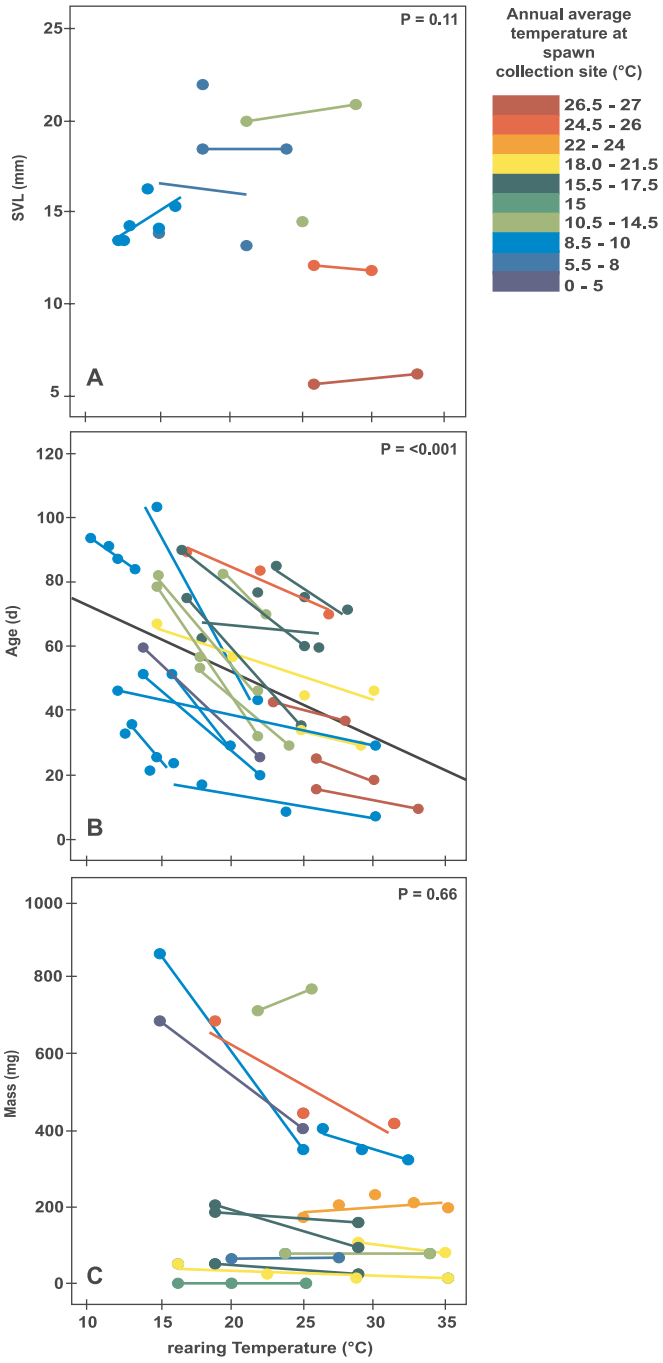


**Fig. 1.** The effect of rearing temperature ($T_{rear}$) on absolute values of **A** snout-vent length (SVL), **B** age, and **C** mass at the onset of metamorphosis. Dots and respective regression lines refer to the individual studies. Black regression line shows the general effect of $T_{rear}$ on dependent variables of all included studies if regression is significant. The color code refers to the annual average temperature (°C) at spawn collection site of respective populations.

20 species key value to have statistical power to distinguish a significant phylogenetic signal value (Blomberg et al., 2003). The nesting followed the Linnean classification (i.e. family/genus/species/population) and addresses the interrelation of datapoints due to varying distances of phylogenetic relatedness.

Before the analysis, the covariates $T_{CM}$ and $T_{HM}$ (i.e. explanatory variables) in the models were tested for covariation using Spearman's rank correlation. Consequentially, all covariates were included in statistical analysis as the correlation was significant but well below the suggested threshold of 0.7 for eliminating variables (N = 69, $R^2$

**Table 1**
Effects of the thermal background ($T_{CM}$ and $T_{HM}$) on plasticity index (PIX) of log-transformed snout-vent length (SVL), mass, and age at the onset of metamorphosis of different anuran species. The plasticity index describes the change in metamorphic traits with a given change in rearing temperature. $T_{CM}$ = Temperature of the coldest month. $T_{HM}$ = Temperature of the hottest month at spawn collection site. N is the total number of included studies, n refers to the number of groups in nested random effects. Random effects were nested for phylogenetic correction.

| Dependent variable | Fixed factor | Linear mixed-effect model | | | | | | Nested random effects (n) | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Estimate | SE | $Chi^2$ | Df | P | N | Species | Genus | Family |
| PIX Age (d) | $T_{HM}$ | −0.071 | 0.001 | 3.521 | 1 | 0.06 | 23 | 18 | 13 | 8 |
| | $T_{CM}$ | −0.073 | 0.001 | 0.172 | 1 | 0.677 | | | | |
| PIX Mass (mg) | $T_{HM}$ | −0.068 | 0.001 | 3.388 | 1 | 0.065 | 15 | 13 | 9 | 5 |
| | $T_{CM}$ | −0.073 | 0.007 | 4.303 | 1 | **0.038** | | | | |
| PIX SVL (mm) | $T_{HM}$ | −0.074 | 0.004 | 0.325 | 1 | 0.568 | 6 | 6 | 5 | 5 |
| | $T_{CM}$ | −0.079 | 0.001 | 27.799 | 1 | < **0.001** | | | | |

= 0.349, P = < 0.001) (Chin, 1998).

## 3. Results

We tested the effect of rearing temperature on age and size at the onset of metamorphosis in anuran larvae performing a combined analysis based on a total of 25 studies. Furthermore, we tested how the thermal background of a population at respective spawn collection site affects the plasticity index (PIX) of metamorphic traits.

### *3.1. Effect of rearing temperature on age and size at the onset of metamorphosis (PIX)*

#### *3.1.1. Age at metamorphosis*

Across all studies, log-transformed age at the onset of metamorphosis (AOM) was significantly, linearly related to temperature (T) according to: AOM = -0.02(T) + 2.11, (N = 23, $R^2$ = 0.218, P < 0.001) indicating that AOM decreased by 0.95 days with every 1 °C increase in rearing temperature (Fig. 1). The highest rearing temperatures led to the youngest age at the onset of metamorphosis and vice versa. On individual study level AOM also decreased as with increasing rearing temperature in 100% of the studies but to different extent (Appendix Table A.1).

#### *3.1.2. Size at metamorphosis*

Across all studies neither log-transformed mass nor SVL at the onset of metamorphosis decreased or increased significantly with rearing temperature (mass: y = -1.01x + 2.65, N = 15, $R^2$ = 0.11, P = 0.66; SVL y = -0.48x + 1.34, N = 6, $R^2$ = 0.16, P = 0.11) (Fig. 1). On individual study level slopes of mass at metamorphosis reveal a decrease with increasing rearing temperature in 75% of the studies, whereas SVL decreased in 50% of the studies (Appendix Table A.1).

### *3.2. Effects of the population-specific thermal background on the PIX of age and size at metamorphosis*

The population-specific thermal background influences the PIX of age, mass, and SVL at the onset of metamorphosis to different extents (Table 1). Generally, the warmer the climate at the spawn collection site, the higher the PIX of age and size at metamorphosis (Fig. 2).

Whereas the $T_{HM}$ marginal significantly affected the PIX of age and mass at the onset of metamorphosis, $T_{CM}$ had a significant effect on the PIX of mass and a highly significant effect on SVL (Fig. 2). The higher the temperatures of the warmest month the higher the PIX of age and mass, whereas the lower the temperatures of the coldest month the lower is the PIX of mass and SVL (Fig. 2).

## 4. Discussion

Temperature has a profound influence on rates of development and growth of ectotherms and, with the ongoing warming of aquatic habitats, a better understanding is needed of the thermal windows supporting growth and survival of organisms. Surprising little work has been made on anurans and our study compiles the available data from 25 different studies to examine general, interspecific relationships between metamorphic traits and temperature. Our results demonstrated that age and size at the onset of metamorphosis are lowest at warmest rearing temperatures and highest at coldest rearing temperatures. Thus, warmer developmental temperatures due to climate change may result in smaller and younger metamorphic larvae. Furthermore, we detected an effect of the population-specific thermal background on the sensitivity of the metamorphic traits with a given change in rearing temperature. Metamorphic traits are less sensitive to changing developmental temperatures in populations adapted to warmer mean temperatures.

### *4.1. Thermal effects on age and size at metamorphosis*

According to Atkinson (1994) there is a very clear instraspecific pattern between growth, size and temperature: most ectotherms at colder temperatures grow slower but reach a larger size than at higher temperatures. Our results confirm this pattern also for different species adapted to different climates but to different extent. Hence, we show that TSR (Atkinson, 1994) is also applicable for across species comparisons, but with some constraints.

In our analysis, age at the onset of metamorphosis was lower at warmer developmental temperatures in all included populations indicating that developmental rate responds plastically to temperature variation independent from respective thermal adaptation. This is obviously due to the general accelerating effects of increasing temperature on physiological and biochemical processes in general and especially on the intensity of THs which are the major triggers of amphibian metamorphosis (Smith-Gill and Berven, 1979; Tata, 2006; Little and Seebacher, 2016). THs are more effective at warmer temperatures during development and their intensity on developmental rate is positively correlated with developmental temperature (Ceusters et al., 1978). This impact of temperature on the TH affects all populations despite their respective thermal adaptation and any stress induced endocrine disruption which may arise due to temperature variation.

Unlike age, no consistent decrease at warmer temperatures was observed in mass or SVL at the onset of metamorphosis. These results for body size demonstrate that the reaction and sensitivity of growth rate are not independent from thermal adaptation. Nevertheless, growth rate is accelerated at warmer temperatures due to the effects of temperature on physiological and biochemical processes (Smith-Gill and Berven, 1979; Tata, 2006; Little and Seebacher, 2016). However, the effecet of temperature on TH appears to have a greater impact on developmental rate as opposed to growth rate (Hayes et al., 1993; Shi, 2000). These two rates can, to some extent, be decoupled by this thermal effect on the intensity of TH (Zuo et al., 2012; Walters and Hassall, 2006; Gomez-Mestre et al., 2010). Furthermore, growth rate was generally less sensitive than developmental rate within our analysis

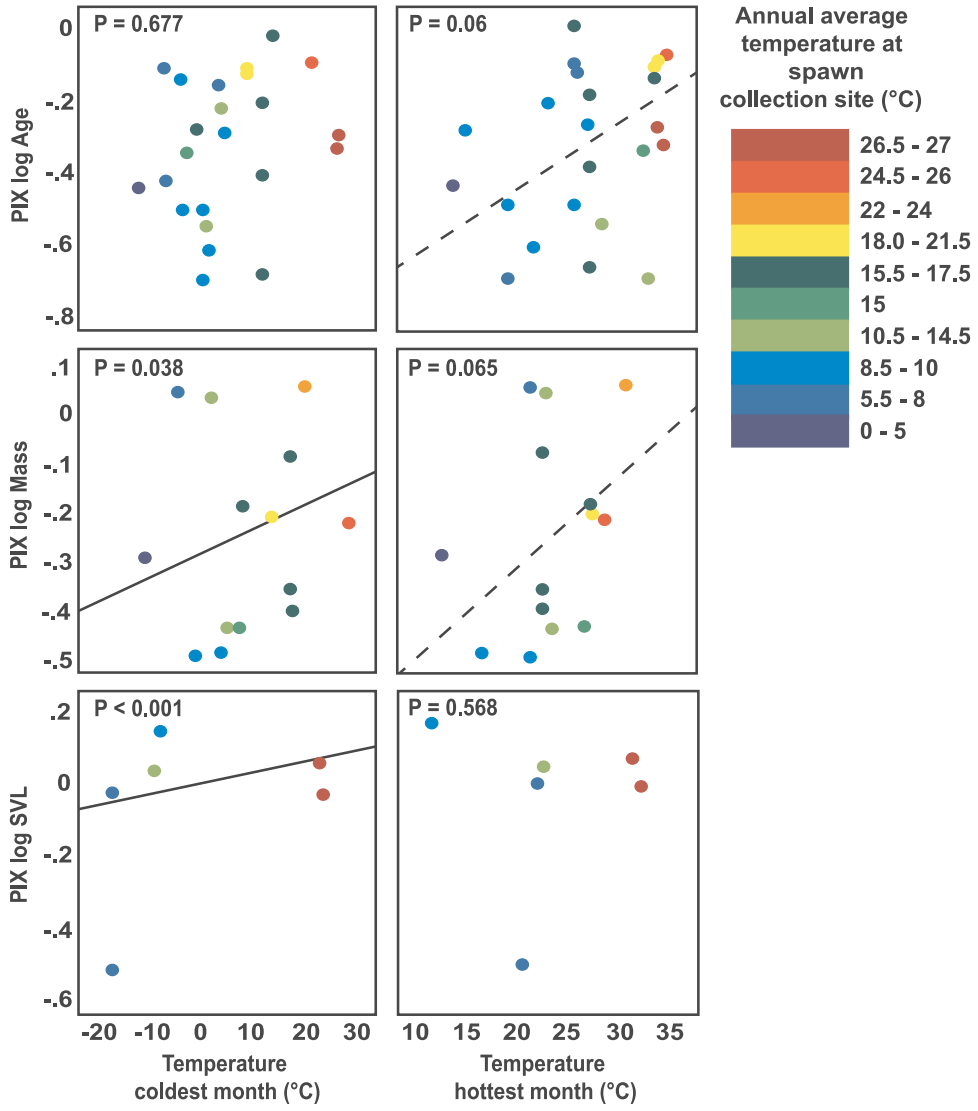


**Fig. 2.** Effects of thermal adaptation ($T_{CM}$ and $T_{HM}$) on plasticity index (PIX) of log-transformed snout-vent length (SVL), mass, and age at the onset of metamorphosis of different anuran species. The plasticity index describes the change in metamorphic traits with a given change in rearing temperature. $T_{CM}$ = Temperature of the coldest month. $T_{HM}$ = Temperature of the hottest month at spawn collection site. The color code refers to the annual average temperature (°C) at spawn collection site of respective populations.

as shown with the PIX. Hence, growth rate is less plastic in response to different constant temperatures than development rate (Atkinson, 1994; Gomez-Mestre et al., 2010). This could be due to the fact that tadpoles must reach a minimal size in order to become metamorphosed (Morey and Reznick, 2000; Rot-Nikcevic and Wassersug, 2004). However, there is no minimum larval duration before metamorphosis sets on as the onset of metamorphosis depends on TH concentration, which has to reach a specific, threshold level (Morey and Reznick, 2000; Buchholz, 2017).

### 4.2. Thermal adaptation affects thermal sensitivity of metamorphic traits

In this analysis, we also investigated whether the population-specific thermal background accounts for the different sensitivity of metamorphic traits to temperature variation as shown by the different plasticity indices for age and size of respective populations. We found that both temperature of the coldest and of the hottest month impact the sensitivity of age and size at the onset of metamorphosis to temperature variation and thus, require the ability for a plastic response in growth and developmental rate. We assume that tadpoles are adapted to the thermal background at respective spawn collection sites.

Our results revealed that populations from colder climates (i.e. low temperatures in the coldest and the hottest month) show lower plasticity indices indicating that development and growth rate are more sensitive to a given change in temperature. Therefore, those populations from colder climates, such as temperate anurans, are more likely to respond plastically in both rates to developmental temperature variation. In contrast, populations adapted to warm temperatures in the coldest and hottest month revealed a lower sensitivity of metamorphic traits to temperature variation indicating a reduced capacity for a plastic response in both growth and developmental rate. Less sensitive growth and developmental rate to changing developmental temperature are common in populations from warmer climates (i.e. tropical climates) due to the relatively stable thermal environments in the tropics (Janzen, 1967; Gunderson and Leal, 2015; Oyamaguchi et al., 2017). However, temperate populations experience more heterogenous thermal environments during their larval stage. Therefore, selection favors a high sensitivity of growth and developmental rate due to temperature variation resulting in a high capacity for a plastic response in both rates (Seebacher et al., 2015).

### 4.3. Fitness consequences

Ecologists generally view the relationship between growth and

development in anuran larvae as an adaptive strategy for coping with selection pressures such as temperature variation (Rose, 2005). In larvae with a reduced capacity for a plastic response in growth and developmental rate as shown for populations from warm climates in our analysis this coping with temperature variations is complicated and limited. As a consequence, negative impacts of temperature variation and extreme thermal events are greatest in warm adapted populations due to the lack of accelerating their developmental rate to avoid overheating or to escape from increased desiccation risk of ephemeral ponds (Gunderson and Stillman, 2015).

Developmental plasticity is adaptive in variable environments (Newman, 1992), but the capacity for a plastic response in growth and developmental rate as a result of temperature variation in larval history leads to different ages and sizes at the onset of metamorphosis which in turn are known to influence fitness in later life stages (i.e. age and size at first reproduction, breeding success, and jumping ability) (Smith-Gill and Berven, 1979; Denver et al., 2002; Altwegg and Reyer, 2003). Individuals with larger body size will tend to have greater performance and fitness than smaller individuals (Berven, 1990; Kingsolver and Huey, 2008). Consequently, a decrease in body size as a result of higher temperatures may be disadvantaged compared to individuals that experience colder temperatures and that reach larger body sizes.

However, growing to and sustaining large size also entails significant costs and risks, as well as delayed maturation and increased energy demands (Kingsolver and Huey, 2008). Only few studies could show the disadvantage of a large body size (but see Wassersug, 1975; Van Buskirk et al., 2017). In terms of energy demand, Beck and Congdon (2000) found that mass at metamorphosis was positively related to metabolic rate, whereas age at metamorphosis was negatively correlated with metabolic rate. Thus, smaller individuals need less energy for energy maintenance (Beck and Congdon, 2000). Particularly under resource limitation smaller individuals are relatively efficient in maintaining somatic functions due to their lower energy demand (Wassersug, 1975). Van Buskirk et al. (2017) emphasizes that consequences of body size depend on the way competing individuals of a group interact. Individuals that metamorphose at a smaller size (i.e. due to higher water temperatures in ponds) may benefit by an earlier escape from predation pressure in their larval habitats but may incur costs such as reduced juvenile survivorship (Smith, 1987; Berven, 1990; Zhao et al., 2014), physiological performance (e.g. the ability to withstand starvation and tolerance to dehydration or to escape predators (Zhao et al., 2014)), as well as reduced fecundity and reduced size at first reproduction (Smith, 1987; Semlitsch et al., 1988; Berven, 1990).

### 4.4. Potential impacts of climate-driven warming

Climate change is increasing mean environmental temperatures and the frequency of extreme thermal events (Seebacher et al., 2015; Pachauri et al., 2014; Gutiérrez-Pesquera et al., 2016). The ability to show developmental plasticity to changing thermal conditions is expected to be a primary factor that dictates the vulnerability of amphibians to rising temperatures (Huey et al., 2012; Stillman, 2003; Gunderson and Stillman, 2015). As we demonstrated in this study, populations developing at warmer mean temperatures show a reduced capacity for a plastic response in growth and developmental rate and therefore, the impacts of climate change may be more severe on those populations or species (Tewksbury et al., 2008; Somero, 2010; Oyamaguchi et al., 2017). However, to predict the vulnerability of a species, we need to determine not only its sensitivity of metamorphic traits, but also the magnitude of exposure to climate-driven warming.

In addition to developmental plasticity, the capacity for physiological acclimation is crucial for organisms to compensate for climate-driven changes in temperature. As shown for growth and developmental rate in our analysis, the capacity for a plastic response in physiological traits (e.g. metabolic rate and thermal limits) is also reduced in warm adapted or rather tropical species due to their narrower thermal window (Huey and Kingsolver, 1993; Angilletta et al., 2002; Pörtner and Peck, 2010). Due to their higher capacity for plastic responses in developmental and physiological traits, temperate species may be less vulnerable to the impact of climate-driven warming (within limits).

Nevertheless, Kingsolver et al. (2015) emphasized that using constant temperature studies to model the consequences of variable thermal environment as caused by to climate change is precarious. Most terrestrial and aquatic ectotherms experience daily and seasonal variation in temperature and then, mean organismal performance can differ in fluctuating and constant thermal environments, an effect due to Jensen's inequality for non-linear functions (Ruel and Ayres, 1999; Martin and Huey, 2008; Kingsolver et al., 2015). Thus, models of ectotherm responses to climate change that are parameterized from data sets gathered under constant (or that assume no change in the variance of thermal regimes) may contain systematic errors when compared with the real world (Helmuth et al., 2010; Paaijmans et al., 2013; see Kearney et al., 2012).

## 5. Conclusion

Climate-driven warming in terms of global change will affect larval anurans, which are especially sensitive to environmental variation due to their life history, their highly permeable skin, and their limited capacity for dispersal. Animals, which are able to exhibit phenotypic plasticity in the timing of metamorphosis within their thermal windows, may escape from those heterogenous and unpredictable larval habitats. Our effort highlights the current lack of data required to thoroughly test how the effect of temperature on developmental traits and data on temperature given developmental plasticity from temperate and tropical amphibians are, however, still too limited to allow for generalized projections on the impacts of climate change at individual and population level. Furthermore, the numerous studies investigating the effect of temperature on metamorphic traits and the sensitivity of metamorphic traits to temperature in terms of thermal adaptation use only 2–3 constant rearing temperatures. These studies are not sufficient to resolve the true shape of the thermal window and the capacity for developmental plasticity according to Kingsolver and Huey (2008). Future studies need to include a broader range of rearing temperatures in order to make robust comments on the developmental plasticity within the thermal window of specific populations or species. In addition, studies need to examine the difference between the effects of temperature fluctuation and different constant temperatures on developmental plasticity in the context of climate change.

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## Conflict of interest

The authors declare that they have no competing interests.

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## Appendix

See Table A.1.

**Table A.1**
Suce effect of temperature on the age and size at metamorphosis in larval anurans. Studies were separated by species as well as by different spawn collection site. Spawn collection site is given as detailed as mentioned in references. $T_{rear}$ = rearing temperature in respective study. $T_{CM}$ = coldest month, $T_{HM}$ = hottest month, $T_{average}$ = annual average temperature at spawn collection site. Plasticity index (PIX) of age and size at the onset of metamorphosis (log-transformed) in different anuran species describing the change in metamorphic traits with a given change in rearing temperature. PIX (i.e., regression slope) was calculated from linear regressions. P and $R^2$ for linear regressions.

| Species | $T_{rear}$ | Spawn collection site | | | | | Plasticity Index | | | | | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Spawn collection site | Coordinates | $T_{CM}$ | $T_{HM}$ | $T_{average}$ | Number of $T_{rear}$ (°C) | Linear Regression | Metamorphic traits | | | |
| | | | | | | | | | Age (d) | Mass (mg) | Snout-vent length (mm) | |
| *Bufo terrestris* | 25<br>30 | Savannah River Site. USA | 32°10'42.7"N<br>81°04'43.9"W | 8.0 | 28.0 | 18.25 | 2 | **PIX** | -0.013 | -0.021 | | Beck and Congdon 2000 |
| *Pelophylax saharicus* | 22<br>24<br>26<br>28<br>30 | Medenine. Tunisia | 33°20'25.4"N<br>10°29'41.2"E | 13.0 | 31.0 | 22.00 | 5 | **PIX**<br>**$R^2$**<br>**P** | | 0.006<br>0.185<br>0.441 | | Bellakhal et al. 2014 |
| *Rana sylvatica* | 10.5<br>11.75 | Dreadful Hollow Pond. Ilex Pond. Southwest Woods Pond. Star Pond. West Marsh Pond. and West Woods Big Pond | 42°36'25.6"N | −4.0 | 22.0 | 9.00 | 4 | **PIX** | −0.015 | | | Benard 2015 |
| | 12.25<br>13.37 | Pinckney. USA | 83°55'50.0"W | | | | | **$R^2$**<br>**P** | 0.979<br>**0.009** | | | |
| *Rana arvalis* | 16<br>20 | Greifswald. Germany | 54°05'07.5"N<br>13°23'23.9"E | 1.0 | 19.0 | 10.00 | 2 | **PIX** | −0.062 | | | Burmeister 2015 |
| *Discoglossus galganoi* | 17<br>25 | Grândola. Portugal | 38°11'29.6"N<br>8°33'59.1"W | 11.0 | 23.0 | 17.00 | 2 | **PIX** | −0.021 | −0.036 | | Carreira et al. 2016 |
| *Hyla arborea* | 17<br>25 | Grândola. Portugal | 38°11'29.6"N<br>8°33'59.1"W | 11.0 | 23.0 | 17.00 | 2 | **PIX** | −0.068 | −0.040 | | Carreira et al. 2016 |
| *Hyla meridionalis* | 17<br>25 | Grândola. Portugal | 38°11'29.6"N<br>8°33'59.1"W | 11.0 | 23.0 | 17.00 | 2 | **PIX** | −0.041 | −0.008 | | Carreira et al. 2016 |
| *Rhacophorus moltrechti* | 17<br>22 | Farmlands in the Wushan area | 23°02'27.6"N | 20.0 | 29.0 | 24.50 | 3 | **PIX** | −0.010 | −0.022 | | Chang et al. 2014 |
| | 27 | Tainan. Taiwan | 120°31'52.8"E | | | | | **$R^2$**<br>**P** | 0.918<br>0.17 | 0.805<br>0.279 | | |
| *Lithobates pipiens* | 23<br>28 | Artificial breeding; Nasco - Fort Atkinson. USA | 56°20'29.9"N<br>2°47'33.6"W | −7.0 | 22.0 | 7.50 | 2 | **PIX** | −0.012 | | | Freitas et al. 2017 |
| *Xenopus laevis* | 18<br>24 | Artificial breeding; Nasco - Fort Atkinson. USA | 56°20'29.9"N<br>2°47'33.6"W | −1.0 | 23.0 | 11.00 | 2 | **PIX** | −0.029 | 0.004 | 0.003 | Gomez-Mestre et al. 2010 |
| *Agalychnis callidryas* | 21<br>29 | Artificial breeding; Boston University | 42°21'02.1"N<br>71°06'33.8"W | −7.0 | 220 | 7.50 | 2 | **PIX** | −0.043 | 0.005 | −0.052 | Gomez-Mestre et al. 2010 |
| *Pseudacris ornata* | 15<br>20<br>25<br>30 | Several breeding ponds on the Savannah River Plant Aiken County. USA | 32°10'42.7"N<br>81°04'43.9"W | 8.0 | 28.0 | 18.00 | 4 | **PIX**<br>**$R^2$**<br>**P** | −0.012<br>0.882<br>0.061 | −0.03<br>0.447<br>0.331 | | Harkey and Semlitsch 1988 |
| *Limnodynastes peronii* | 13<br>14.2<br>15 | Greater Illawarra region of south-eastern New South Wales. Australia | 34°26'00.0"S<br>150°51'00.0"E | 13.0 | 22.0 | 17.50 | 3 | **PIX**<br>**$R^2$**<br>**P** | −0.002<br>0.027<br>0.906 | | | Courtney Jones et al. 2015 |
| *Rana temporaria* | 12.2<br>12.7<br>13.1 | Ponds in southwestern and central Scania. province Skåne | 55°42'18.1"N | 0.0 | 17.0 | 8.50 | 6 | **PIX** | −0.071 | | 0.015 | Loman 2002 |
| | 14.5<br>14.9<br>16.1 | Lund. Sweden | 13°11'29.3"E | | | | | **$R^2$**<br>**P** | 0.746<br>**0.032** | | 0.488<br>0.129 | |
| *Rhinella granulosa* | 26<br>33 | Temporary ponds at the campus of the Universidade Estadual de Feira de Santana Feira de Santana. Brazil | 12°15'11.9"S<br>38°57'53.6"W | 25.0 | 28.5 | 26.75 | 2 | **PIX** | −0.034 | | −0.003 | Maciel and Juncá 2009 |
| *Pleurodema diplolister* | 26<br>30 | Temporary ponds at the campus of the Universidade Estadual de Feira de Santana Feira de Santana. Brazil | 12°15'11.9"S<br>38°57'53.6"W | 25.0 | 28.0 | 26.50 | 2 | **PIX** | −0.030 | | 0.005 | Maciel and Juncá 2009 |
| *Rana perezi* | 19.5<br>22.5 | Pond in Chozas de Arriba. Spain | 42°31'17.5"N<br>5°42'01.0"W | 3.0 | 20.0 | 11.5 | 2 | **PIX** | −0.023 | | | Martinez et al. 1996 |

(*continued on next page*)

**Table A.1** (*continued*)

| Species | $T_{rear}$ | Spawn collection site | | | | | Plasticity Index | | | | | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Spawn collection site | Coordinates | $T_{CM}$ | $T_{HM}$ | $T_{average}$ | Number of $T_{rear}$ (°C) | Linear Regression | Metamorphic traits | | | |
| | | | | | | | | | Age (d) | Mass (mg) | Snout-vent length (mm) | |
| *Rana temporaria* | 14<br>22 | Lund. Sweden | 55°42'18.1"N<br>13°11'29.3"E | 0.0 | 17.0 | 8.5 | 2 | **PIX** | −0.051 | −0.049 | | Merilä et al. 2000 |
| *Rana temporaria* | 14<br>22 | Kiruna. Sweden | 67°51'34.7"N<br>20°13'25.7"E | -12.0 | 13.0 | 0.5 | 2 | **PIX** | −0.052 | −0.029 | | Merilä et al. 2000 |
| *Rana sylvatica* | 15<br>18<br>22 | Saginaw Forest. University of Michigan. USA | 42°16'13.2"N<br>83°48'23.4"W | -4.0 | 22.0 | 9.0 | 3 | **PIX**<br>**$R^2$**<br>**P** | −0.056<br>0.994<br>0.262 | −0.05<br>0.957<br>**0.05** | | Riha and Berven 1991 |
| *Rana sylvatica* | 15<br>18<br>22 | The Shenandoah Mountains. USA | 38°29'28.2"N<br>78°50'52.0"W | 1.0 | 24.0 | 12.5 | 3 | **PIX**<br>**$R^2$**<br>**P** | −0.036<br>0.995<br>**0.026** | −0.044<br>0.972<br>0.107 | | Riha and Berven 1991 |
| *Rana sylvatica* | 15<br>18<br>22 | Beltsville Agricultural Research Station. USA | 39°01'32.2"N<br>76°55'23.1"W | 3.0 | 27.0 | 15.0 | 3 | **PIX**<br>**$R^2$**<br>**P** | −0.03<br>0.873<br>0.098 | −0.044<br>0.998<br>**0.03** | | Riha and Berven 1991 |
| *Xenopus laevis* | 18<br>24<br>30 | Artificial breeding; St Andrews University. Scotland | 56°20'29.9"N<br>2°47'33.6"W | 4.0 | 14.0 | 9.0 | 3 | **PIX**<br>**$R^2$**<br>**P** | −0.015<br>0.979<br>0.265 | | | Walsh et al. 2008 |
| *Rana sylvatica* | 15<br>18<br>21 | Tzfardeyah Pond at Warner Nature Center Marine on St. Croix. USA | 45°10'21.6"N<br>92°49'54.2"W | -8.0 | 23.0 | 7.5 | 3 | **PIX**<br>**$R^2$**<br>**P** | | | −0.003<br>0.4<br>0.950 | Watkins and Vraspir 2005 |
| *Rana chensinensis* | 23.2<br>25.3<br>28.1 | Xinyang. China | 32°09'04.5"N<br>114°05'05.2"E | 3.0 | 28.0 | 15.5 | 3 | **PIX**<br>**$R^2$**<br>**P** | −0.016<br>0.91<br>0.207 | −0.019<br>0.930<br>0.171 | | Yu et al. 2015 |

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